

Orientation in the wandering albatross: interfering with magnetic perception does not affect orientation performance

F. Bonadonna^{1*}, C. Bajzak¹, S. Benhamou¹, K. Igloi¹, P. Jouventin¹, H. P. Lipp² and G. Dell’Omo²

¹*Behavioural Ecology Group, CNRS-CEFE, 1919 route de Mende, F-34293 Montpellier Cedex 5, France*

²*Division of Neuroanatomy and Behavior, Institute of Anatomy, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland*

After making foraging flights of several thousands of kilometres, wandering albatrosses (*Diomedea exulans*) are able to pinpoint a specific remote island where their nests are located. This impressive navigation ability is highly precise but its nature is mysterious. Here we examined whether albatrosses rely on the perception of the Earth’s magnetic field to accomplish this task. We disturbed the perception of the magnetic field using mobile magnets glued to the head of nine albatrosses and compared their performances with those of 11 control birds. We then used satellite telemetry to monitor their behaviour. We found that the ability of birds to home to specific nest sites was unimpaired by this manipulation. In particular, experimental and control birds did not show significant differences with respect to either foraging trip duration, or length, or with respect to homing straightness index. Our data suggest that wandering albatrosses do not require magnetic cues to navigate back to their nesting sites.

Keywords: magnetic orientation; navigation; albatross; homing

1. INTRODUCTION

Since the seminal report by Jouventin & Weimerskirch (1990) on the impressive foraging flights of wandering albatrosses, it has been suggested that the orientation mechanism underlying such long-range navigation in absence of any topographical cues could be the Earth’s magnetic field (Åkesson 1996). During the breeding season, wandering albatrosses leave their small breeding island to set out on foraging flights. These flights span distances of several thousands of kilometres. Birds may be away from the nest for several weeks, foraging in all quadrants around the island both en route and at their destination (Weimerskirch *et al.* 1993, 1994). After such foraging trips over foggy and ‘featureless’ oceans, however, they are able to return to their home with surprising precision. Unlike migrating birds (Berthold 1991), albatrosses are not likely to rely on a genetic programme. These programmes specify the compass bearing at different times to navigate between established summer and winter quarters. Genetic programmes cannot, therefore, be applied to navigate between albatrosses’ foraging areas and reproductive sites, because the locations of the foraging areas vary frequently.

The idea that an animal can rely on the Earth’s magnetic field for orientation purposes is supported by several examples. Passerine birds have been shown to rely on a magnetic compass during migration (Wiltschko & Wiltschko 1972, 1996) while homing pigeons become disoriented in sites where magnetic anomalies exist, or when they have magnets experimentally attached to their

heads (Luschi *et al.* 1996; Wiltschko & Wiltschko 1996; but see Wallraff 1999). Among aquatic species, spiny lobsters (*Palinurus argus*) have been shown to derive positional information from the Earth’s magnetic field (Boles & Lohmann 2003). Moreover, both hatchling and juvenile sea turtles (*Caretta caretta*) can detect the angle of inclination and the total intensity of the geomagnetic vector (Lohmann *et al.* 2001, 2004). Whether adults use these cues is still under debate (Papi *et al.* 2000). While the mechanism underlying magneto-reception is still unknown for any animal, several recent reports have linked this perceptual ability to the visual system (Wiltschko *et al.* 2002; Ritz *et al.* 2004).

In the southern oceans where islands are scarce, wandering albatrosses lack visual topographical landmarks to fix their position, both solar and star compasses are often obscured by cloudy skies. Therefore, albatrosses may use magnetic cues, both for map and compass steps, to find their way over the oceans.

Although evidence for the use of earth-strength magnetic fields is convincing for many animals, the situation with albatrosses is less clear. Åkesson & Alerstam (1998) have investigated whether any combination of different geomagnetic parameters might provide a reliable bi-coordinate map suitable for albatrosses’ navigation. Their findings indicate that the use of a geomagnetic bi-coordinate map could be possible only in some areas over the open oceans.

Bonadonna, Chamaille-Jammes *et al.* (2003b) showed that magnetically disturbed black-browed albatrosses, *Diomedea melanophrys*, breeding in the Kerguelen Islands, did not differ significantly from control birds in foraging

* Author for correspondence (bonadonna@cefe.cnrs.fr).

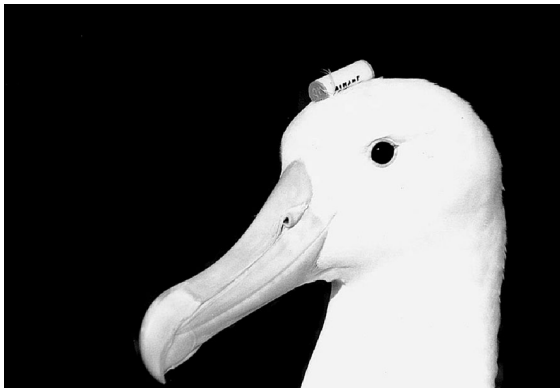


Figure 1. Wandering albatross with a head-mounted plastic box containing a mobile magnet.

trip duration, even though birds carrying magnets consistently had longer foraging trips than control birds. In the absence of tracked foraging paths, this result suggests that depriving birds of magnetic cues may impact their initial ability to navigate or forage, but birds are able to compensate for this loss. For example, it is possible that birds become disoriented at first, but shift to a complementary mechanism if the magnetic sense is disrupted. Whether this is true cannot be determined without fine-scale monitoring of foraging tracks. Moreover, black-browed albatrosses perform much shorter trips than wandering albatrosses do, and forage at the limit of the Kerguelen plateau (Weimerskirch *et al.* 1997). Thus, one can argue that birds in this particular study were always relatively close to the nesting colony and may have easily been able to shift between different orientation systems, depending on the circumstances (Bonadonna, Benhamou *et al.* 2003a).

Mouritsen *et al.* (2003) demonstrated that the attachment of magnets to the head of waved albatrosses, *Phoebastria irrorata*, breeding on the Galapagos Islands did not affect their orientation abilities. However, there were several problems with this preliminary study. First, magnets were fixed in place such that birds could have compensated for the effect of the manipulation (Wiltschko 1978; Wiltschko & Wiltschko 1996). Second, most of the birds lost magnets en route (probably before the homing trip, as discussed by the authors), making results difficult to interpret. Finally, subjects tended to begin their homing flights when they were close to the South American coast, which may provide numerous potential cues about their position with respect to the goal. The results of these two studies, hence, do not exclude that magnetic perception can play a primary role in albatrosses' navigation.

In this study we examined the use of magnetic navigation in the most widely ranging seabird, the wandering albatross (*Diomedea exulans*). We studied birds nesting in the Kerguelen Islands in the Southern Indian Ocean. These birds forage in areas that are completely pelagic with no visible topographical landmarks to aid them in orientation. Islands are scarce in this area (the closest islands are: Heard at 500 km south-east, St Paul and New Amsterdam at 1300 km north-east, Crozet at 1400 km west; the closest continental landmass is Antarctica at 2000 km south). Birds were individually tracked using a combination of satellite telemetry and global positioning to monitor fine-scale movement. We

predicted that if birds relied substantially on geomagnetic cues, then disturbing this sense would cause a measurable distortion in their flight paths compared to control birds. In particular, we predicted that homing efficiency (as measured by a straightness index) should be lower, while path tortuosity should be higher in experimental than in control birds.

2. MATERIAL AND METHODS

(a) General procedures

The study was carried out in the Kerguelen archipelago (49.25 S, 70.50 E). This area is a particularly suitable place for studying orientation abilities of albatrosses because there are no continental land masses in a radius of 2000 km, and islands are rare. During the albatrosses' incubation and brooding periods (March to May 2003), 20 albatrosses were captured at their nests and equipped with platform transmitters terminals (PTT, Argos system) and satellite tracking devices or Global Positioning System (GPS) data loggers (Steiner *et al.* 2000; Weimerskirch *et al.* 2002). Birds were at least 10 years old (mean age of first breeding; Brooke 2004).

Birds in our experimental group (7 PTT and 2 GPS) were equipped with a cylindrical neodymium magnet, tumbling freely within a PVC container glued on the head (figure 1). Magnets (type Neo35, diameter 4 mm, length 27 mm; Calamit, Milan, Italy) have a nominal residual induction of 1.17–1.22 T. At 15 cm from the magnet, the field is still strong enough to overshadow the natural magnetic field in Kerguelen (*ca* 48 000 nT). The PVC box containing the magnet was attached to the head feathers of the bird using cyanoacrylate glue. Magnets by themselves have been shown to disrupt magneto-reception in both other birds (homing pigeons; Keeton 1971) and reptiles (hatchling sea turtles; Irwin & Lohmann 2003). However, birds, when submitted to a fixed disruption of the magnetic field, can compensate for this disruption and thus recover their magnetic compass (Wiltschko 1978; Wiltschko & Wiltschko 1996). By contrast, allowing the magnet to rotate freely in space imposes unpredictable variations in the direction of the magnetic vector, and thus prevents any possibility of recalibration. Albatrosses were therefore prevented from using a magnetic compass and/or a hypothetical magnetic map. Control birds (8 PTT and 3 GPS) were fitted with similar devices except that the magnet was replaced with a non-magnetic brass bar. Both sexes were evenly represented in each group. After being equipped with the tracking device, treated and control birds were released near their nest. Equipped birds left for their foraging trips in the 2–3 h following this manipulation.

(b) Tracking devices

PTT transmitters were 25 g. PTT100 (Microwave Telemetry, Inc.) packaged by Sirtrack Ltd, New Zealand. Location data are obtained once every 2 h with a mean accuracy of about 1 km.

The GPS data loggers (62×32×14 mm) consisted of GPS receivers with integrated antenna and an eight Mbit flash memory operated by a rechargeable battery (NewBehavior, Hardturmstrasse 76, CH-8005 Zürich; www.newbehavior.com). The loggers were sealed into small, polyethylene bags (thickness 0.4 mm) and were protected by

a light waterproof plastic case. The overall weight of this waterproof package, including batteries, was 80 g. Location data were recorded and computed at 1 s intervals for 3 min every hour, with a mean accuracy of about 10 m.

Both devices (less than 1% of the bird's weight) were attached on the back of the bird with marine tape (Tesa number 4651). The analysis of foraging trips was performed at two levels: general (PTT and simplified GPS data, see below) and detailed (complete GPS data).

(c) *Defining the homing path*

It is difficult to distinguish between the outward leg and the inward (homing) leg in a loop foraging trip. Consequently, we were not able to define for certain a point at which a given albatross decided to fly home. Since the homing path should be the most crucial part of the trip for assessing any disruptions to navigation abilities, our first task was to define a homing start point for each bird. The location at which an animal started orientating toward the goal was first determined using a backward path analysis (starting at the goal location and moving backward along the path) as the point where the backward current beeline distance (BD) stops increasing linearly with respect to the backward path length (BL; see figs. 2 and 3 in Girard *et al.* 2004 for details). The orientation efficiency was computed as the ratio BD:BL (straightness index) measured at this location. This type of analysis assumes that the path length travelled towards a goal is proportional to the BD between an animal's current location and the goal, irrespective of the orientation mechanism being employed (Benhamou & Bovet 1992; Benhamou 2004). As there exists some subjectivity in visually determining the shift from a linear to a nonlinear relationship, comparisons between experimental and control homing paths based on backward path analysis might be somewhat biased. Thus, to validate our analysis, we repeated comparisons defining alternative homing paths (by other blind criteria) as the last 20, 25 and 30% of the trip. In addition, we analysed the path taken by birds from 90% of the furthest distance from the colony. This allowed us to obtain five unique 'homing' start points for each albatross.

(d) *Large-scale tracking data analysis*

In order to compare the general parameters of the foraging trips, we used path information obtained from both the PTT transmitters and GPS loggers. For this general analysis, we simplified the GPS data by considering only one location per hour.

Considering the foraging trip as a whole, we performed Mann–Whitney *U*-tests to compare the following parameters between control and experimental birds: foraging trip duration (trip time), total path length (distance covered), maximum BD from the colony and mean flight speed. We also compared the homing portions of the trips between groups by Mann–Whitney *U*-tests, with respect to the following general parameters: BD, mean speed and straightness index. To determine whether control and experimental birds differed significantly with respect to homing strategies, we compared homing start-point distributions using Hotelling tests. To determine whether the backward path analysis introduces a bias, each comparison between control and experimental birds was performed for each of the five homing criteria.

(e) *Fine-scale tracking data analysis*

We took advantage of the high spatial resolution of the GPS

data (obtained at the rate of one location per second for 3 min every hour) to check possible differences between experimental and control birds. GPS data were normalized by spatial 'rediscretization' with a constant step length of 100 m (Bovet & Benhamou 1988). This method consists of resampling–interpolating the recorded paths so that any two successive locations are 100 m apart. We then performed a small-scale path analysis by focusing on data sets spanning at least 500 m (five steps), hereafter referred to as 'GPS-sets'. For each of these sets, we measured the local path tortuosity (*T*) as

$$T = 1 - C,$$

where *C* is the mean cosine of changes of direction (Benhamou 2004). In addition, for data sets describing the homing path determined by backward path analysis, we measured (both globally and only for night flight) the local orientation performance as the local straightness index *D/L*, where *D* is the difference between the initial and final BDs to home, and *L* is the path length travelled during the 3 min set (Benhamou 2004).

3. RESULTS

All albatrosses returned safely. During our study, most experimental and control birds embarked upon relatively short trips, lasting 50–100 h and covering 1000–2000 km. However, two of the magnet-bearers set-off on trips of 6000–8000 km, travelling in a big loop that eventually brought them back to the nest site. From the point where the birds presumably decided to return home, the flight path was relatively straight (figures 2 and 3). Plastic boxes containing magnets or brass bars were still present on all birds upon return.

(a) *Large-scale tracking data analysis*

General flight parameters of foraging trips were not statistically different between the two treatments except with respect to mean speed. Experimental birds moved significantly faster on average (table 1). With respect to the homing leg of the flight, we found no significant differences in straightness index, BD, and mean speed between control and experimental birds (table 1). The distributions of start points for homing were also similar between experimental and control birds (Hotelling test $F_{2,17} < 1$, n.s.), suggesting that there was no systematic bias in approaching the island due to a particular seamark or a visual property of the ocean. Significance levels are similar across the five homing criteria.

(b) *Fine-scale tracking data analysis*

The homing portion defined by using backward path analysis did not seem to introduce a bias and so we used this method to make comparisons between the two treatments groups. In general, navigational uncertainty is associated with increased tortuosity and meandering of the flight path (Guilford *et al.* 2004; Roberts *et al.* 2004). With only two experimental birds and three control birds equipped with GPS loggers, we were not able to statistically compare experimental and control birds using individual birds as the source of variation. However, such comparisons could be made at the 'GPS-set' level (i.e. irrespective of the individuals involved) provided that

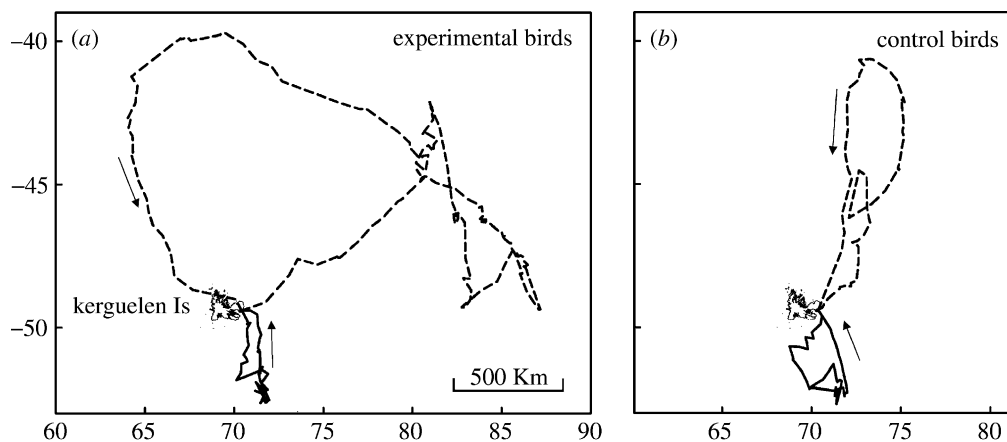


Figure 2. One long and one short trip for (a) experimental (respectively, 8260 and 1509 km covered) and (b) control (respectively, 2875 and 1564 km covered) albatrosses. Arrows indicate the home course.

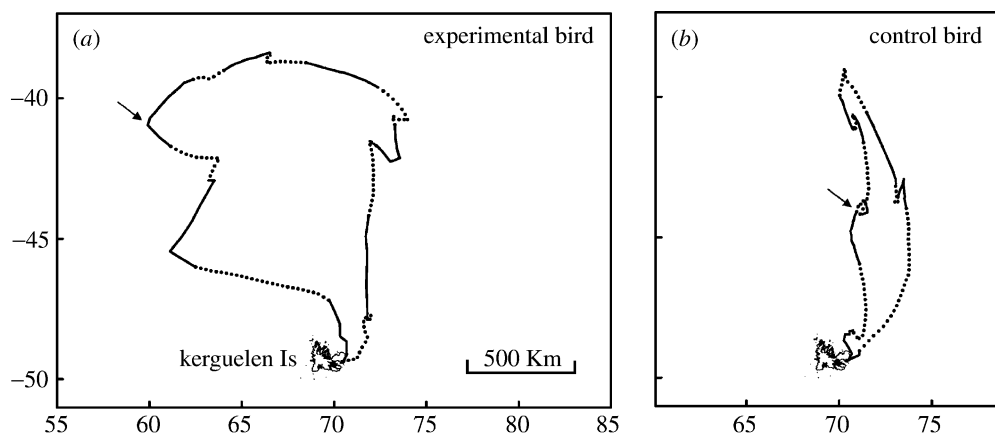


Figure 3. Tracks of (a) an experimental (4672 km covered) and (b) a control (3236 km covered) wandering albatross nesting in the Kerguelen Islands. Dotted lines represent the parts of the trip flown during the night. An arrow indicates the homing start point calculated by backward path analysis (see §2).

GPS-sets proved to be statistically homogeneous among individuals of each group. Using ANOVAs, we showed that neither the mean tortuosity (experimental birds $F_{1-177}=0.27$, n.s.; control birds $F_{2-234}=0.00$, n.s.) nor the mean straightness index for the homing trip (experimental birds $F_{1-47}=2.04$, n.s.; control birds $F_{2-57}=0.19$, n.s.) differed significantly in homogeneity. Similarly, the night parts of the homing trip (experimental birds $F_{1-20}=0.13$, n.s.; control birds $F_{2-22}=0.22$, n.s.) obtained for the different birds in each group did not differ significantly in homogeneity. Consequently, we were able to compare control and experimental birds at the GPS-set level to determine a possible effect of magnetic disturbance. Comparing path tortuosity for the foraging trips, we found that control birds moved in more tortuous paths than magnetically disturbed birds did (mean \pm s.e.: experimental bird 0.19 ± 0.01 , control birds 0.25 ± 0.01 ; $F_{1-414}=16.10$, $p < 0.01$). With respect to the homing portion of the trip, we also found that the local straightness index differed significantly between the two groups: mean \pm s.e.: experimental bird 0.58 ± 0.05 , control birds 0.41 ± 0.06 ; $F_{1-107}=3.50$, n.s. This remained true when considering nocturnal homing flight portions only: mean \pm s.e.: experimental bird 0.60 ± 0.07 , control birds 0.41 ± 0.08 ; $F_{1-56}=1.69$, n.s. (figure 3). Thus, by at least

two parameters, birds carrying magnets tended to fly straighter paths than control birds.

4. DISCUSSION

Our results indicate that magnetic disturbance did not pose major navigation problems to wandering albatrosses foraging over the open ocean. These results support findings of other researchers in suggesting that albatrosses and petrels do not rely exclusively on magnetic cues for long-distance navigation (Benhamou *et al.* 2003; Bonadonna, Chamaille-Jammes *et al.* 2003b; Mouritsen *et al.* 2003). Moreover, in our experiment shortcomings of the previous works were avoided.

Wandering albatrosses forage pelagically in areas where there are no visual topographical landmarks. Magnetic cues might have a relevant role in their orientation by providing them with a magnetic compass (directional sense) and/or a magnetic map (locational sense). The ability to use these cues could assist albatrosses in behaviours that require precise navigation, as when birds need to fly back to breeding colonies to relieve partners or provision hungry chicks on the nest. Our results, however, suggest that disrupting the magnetic field around a wandering albatross's head has no influence on the ability to home, suggesting that birds use other sensory modalities to

Table 1. Large-scale trip parameters of experimental and control wandering albatrosses.

(First group of parameters refer to whole foraging trip, second group to homing trip calculated by backward path analysis (see §2). *U* refers to Mann–Whitney *U* statistic; **p* < 0.05.)

parameter (unit)	experimental (N=9)				control (N=11)				
	min	max	mean	s.e.	min	max	mean	s.e.	<i>U</i>
trip time (h)	56	293	140	23.4	42	241	115.5	18.4	62
distance covered (km)	1509	8260	3565	695	730	3511	2009	278	75
max beeline distance (km)	370	1297	742	108	265	1003	543	75	70
mean speed (km h ⁻¹)	12.1	36.3	25.8	2.5	10.9	25.2	18.6	1.5	80*
global straightness index	0.64	0.84	0.74	0.02	0.55	0.94	0.78	0.03	38
homing beeline distance (km)	299	1297	607	111	167	926	452	67	66
homing mean speed (km h ⁻¹)	10.8	47.4	28.5	4.7	7.8	35.9	19.1	2.3	66

acquire locational and directional information. We cannot rule out that albatrosses possess an unidentified organ for navigationally relevant magneto-perception in part of their body, such as the caudal parts, more distant than 15 cm from the magnet, although this appears unlikely in view of recent reports of magnetic sensing through the visual system of migratory birds (Wiltschko *et al.* 2002; Ritz *et al.* 2004).

Birds have been shown to determine directional information using magnetic cues (Wiltschko & Wiltschko 1996), but other cues also come into play. It is well established that many species preferentially use a sun compass or celestial cues, when available, over the magnetic compass (Wiltschko & Wiltschko 2003). It is thus likely that wandering albatrosses prefer to use sun-compass orientation even if magnetic cues are available to them. With respect to the sun compass, most of the albatrosses we tested completed their foraging trips under 60–80% of cloud cover (data from NOAA NCEP-NCAR CDAS, <http://iridl.ldeo.columbia.edu/SOURCES/.NOAA>). It is generally assumed that this amount of cloud cover does not preclude the use of a sun compass. Although there is conflicting evidence that birds of any species can detect the plane of polarization of light (Martin 1991), the current hypothesis is that even 80% cloud coverage allows birds access to sufficient polarized light to extrapolate the position of the sun in the sky (Phillips & Waldvogel 1988; Cochran *et al.* 2004). At night, many species of bird are able to orient using star configurations (Mouritsen & Larsen 2001; Wiltschko & Wiltschko 2003). Here, studies have primarily been carried out in migratory species that can be easily manipulated to orient under laboratory conditions where their perception of the night sky can be altered (Emlen 1970; Able & Able 1990). In contrast to polarized sunlight patterns, star configurations are easily obscured under conditions of near total cloud cover. Still, we cannot rule out the possibility that our albatrosses were able to navigate using celestial cues.

Navigation in albatrosses requires both locational sense (a sense of knowing where one is) and directional sense (a sense of knowing in which direction to fly). Indeed, since wandering albatrosses do not commute between the breeding island and a fixed foraging area, the homing direction is not fixed but largely depends on the bird's immediate location. Since magnets affected magneto-reception globally, our results further suggest that the locational sense is not primarily based on magnetic

cues. Indeed, if albatrosses rely primarily on the magnetic map sense proposed for turtles (Lohmann *et al.* 2004), and the magnetic detection system is located in the head (Wiltschko *et al.* 2003), we should have obtained some clear effects gluing mobile magnets to the head. Similarly, that homing capacities of pigeons from unfamiliar areas can be completely disrupted by preventing the birds from smelling atmospheric odours indicates that the olfactory map is the principal orientation mechanism for these birds (Wallraff 2001, 2004). Unlike the birds of Mouritsen *et al.* (2003), our albatrosses had very few opportunities to see land, and none of them approached any of the few islands in that part of the ocean during their trip (the closest approach to the Crozet archipelago, 46.5 S–52.2 E, was 715 km and to Heard Island, 53 S–73.5 E, was 115 km). However, ocean swells, boundaries between water masses or odours gradients might have provided cues for orientation (Bonadonna, Benhamou *et al.* 2003a). During the night, albatrosses can no longer rely on potential daylight cues (e.g. sea colour, other birds, etc.). Night vision seems to be poorly developed in the few species that have been studied (Warham 1996). Chemical cues, or even infrasound (Kreithen 1978; Hagstrum 2000) appear to be best candidates for albatrosses orientation. The possibility that a magnetic sense contributes to a multi-modal system for location fixing remains to be shown (Able 1996; Walcott 1996).

Finally, the head-mounted mobile magnets had no discernible negative effect on homing ability from short and long distances. The fact that two experimental birds homed almost in a beeline from a distance of more than 1000 km over a featureless ocean is a strong argument against magnetic navigation. It is unlikely that the magnetic disturbance produced by our manipulations instigated the long-range flights, since one might predict that such disturbance would also have impaired the successful homing. Moreover, the experimental and control groups did not seem to rely on different strategies to perform their foraging trips. In particular, magnetically disturbed birds did not tend to forage closer to the breeding island to minimize the risk of being lost and did not start their homing flight in areas that were different from the start points of the control birds (as revealed by Hotelling tests).

The lower sinuosity and the higher speed that we observed in experimental birds are unexpected. Experimental birds travelled in straighter paths than control

birds and this is the opposite of what one would expect if the magnets disrupted navigational ability. Still, the significance of this finding is unknown but this result cannot suggest that experimental birds were less efficient than control birds in orientation.

The significance of our findings is twofold. First, our results challenge the idea that magnetic navigation is used as a primary navigational aid by pelagic albatrosses. The second point is perhaps even more interesting: if it is not by means of the magnetic field, how can they do it? What sense or system enables these birds to cross thousands of kilometres for foraging and still find home so precisely? Many Procellariiformes have developed an excellent sense of smell (Nevitt *et al.* 1995; Nevitt 1999, 2000; Bonadonna & Bretagnolle 2002; Bonadonna, Hesters *et al.* 2003c; Bonadonna *et al.* 2004) and albatrosses in particular have a well developed olfactory system (Bang 1966; Warham 1996). Albatrosses and other petrels may rely more heavily on olfactory maps both to forage and in long-distance navigation (Nevitt 1999; Wallraff & Andreae 2000; Bonadonna, Benhamou *et al.* 2003a; Nevitt & Bonadonna *in press*). Thus, we believe that the disregard of albatrosses for geomagnetic cues opens interesting research perspectives for biologists.

We are grateful to the 'Institut Polaire Français Paul Emile Victor' (IPEV) for financial and logistical support. This study was also supported by Swiss National Science Foundation and the NCCR 'Neural Plasticity and Repair'. The Ethical Committee from IPEV approved the study. We are also grateful to Prof. T. Alerstam, Prof. G.A. Nevitt, and three anonymous referees for valuable comments on the manuscript. The photograph of figure 1 has been kindly provided by C.B.

REFERENCES

- Able, K. P. 1996 The debate over olfactory navigation by homing pigeons. *J. Exp. Biol.* **199**, 121–124.
- Able, K. P. & Able, M. A. 1990 Calibration of the magnetic compass of migratory bird by celestial rotation. *Nature* **347**, 378–380.
- Åkesson, S. 1996 Geomagnetic map used for long-distance navigation? *TREE* **11**, 398–400.
- Åkesson, S. & Alerstam, T. 1998 Oceanic navigation: are there any feasible geomagnetic bi-coordinate combinations for albatrosses? *J. Avian Biol.* **29**, 618–625.
- Bang, B. G. 1966 The olfactory apparatus of tubenosed birds (Procellariiformes). *Acta Anat.* **65**, 391–415.
- Benhamou, S. 2004 How to reliably estimate the tortuosity of an animal's path: straightness, sinuosity or fractal dimension? *J. Theor. Biol.* **229**, 209–220.
- Benhamou, S. & Bovet, P. 1992 Distinguishing between elementary orientation mechanisms by means of path analysis. *Anim. Behav.* **43**, 371–377.
- Benhamou, S., Bonadonna, F. & Jouventin, P. 2003 Successful homing of magnet-carrying white-chinned petrels released in the open sea. *Anim. Behav.* **65**, 729–734.
- Berthold, P. 1991 Spatiotemporal programmes and genetics of orientation. *Orientation in birds* (ed. P. Berthold), pp. 86–105. Berlin: Birkhauser Verlag.
- Boles, L. C. & Lohmann, K. J. 2003 True navigation and magnetic maps in spiny lobsters. *Nature* **421**, 60–63.
- Bonadonna, F. & Bretagnolle, V. 2002 Smelling home: a good solution for burrow finding in nocturnal petrels? *J. Exp. Biol.* **205**, 2519–2523.
- Bonadonna, F., Benhamou, S. & Jouventin, P. 2003a Orientation in "featureless" environments: the extreme case of pelagic birds. In *Avian migration* (ed. P. Berthold, E. Gwinner & E. Sonnenschein), pp. 367–377. Berlin: Springer.
- Bonadonna, F., Chamaillé-Jammes, S., Pinaud, D. & Weimerskirch, H. 2003b Magnetic cues: are they important in black-browed albatross *Diomedea melanophrys* orientation? *Ibis* **145**, 152–155.
- Bonadonna, F., Hesters, F. & Jouventin, P. 2003c Scent of a nest: discrimination of own-nest odours in Antarctic prions (*Pachyptila desolata*). *Behav. Ecol. Sociobiol.* **54**, 167–173.
- Bonadonna, F., Villafane, M., Bajzak, C. & Jouventin, P. 2004 Recognition of burrow's "olfactory signature" in blue petrels, *Halobaena caerulea*: an efficient discrimination mechanism in the dark. *Anim. Behav.* **67**, 893–898.
- Bovet, P. & Benhamou, S. 1988 Spatial analysis of animals' movements using a correlated random walk model. *J. Theor. Biol.* **131**, 419–433.
- Brooke, M. d. L. 2004 *Albatrosses and petrels across the world*. New York: Oxford University Press.
- Cochran, W. W., Mouritsen, H. & Wikelski, M. 2004 Migrating songbirds recalibrate their magnetic compass daily from twilight cues. *Science* **304**, 405–408.
- Emlen, S. T. 1970 Celestial rotation: its importance in the development of migratory orientation. *Science* **170**, 1198–1201.
- Girard, C., Benhamou, S. & Dagorn, L. 2004 FAD: Fish Aggregating Device or Fish Attracting Device? A new analysis of yellowfin tuna movements around floating objects. *Anim. Behav.* **67**, 319–326.
- Guilford, T., Roberts, S., Biro, D. & Rezek, I. 2004 Positional entropy during pigeon homing. II. Navigational interpretation of Bayesian latent state models. *J. Theor. Biol.* **227**, 25–38.
- Hagstrum, J. T. 2000 Infrasound and the avian navigational map. *J. Exp. Biol.* **203**, 1103–1111.
- Irwin, W. P. & Lohmann, K. J. 2003 Magnet-induced disorientation in hatchling loggerhead sea turtles. *J. Exp. Biol.* **206**, 497–501.
- Jouventin, P. & Weimerskirch, H. 1990 Satellite tracking of wandering albatrosses. *Nature* **343**, 746–748.
- Keeton, W. T. 1971 Magnets interfere with pigeon homing. *Proc. Natl Acad. Sci. USA* **68**, 102–106.
- Kreithen, M. L. 1978 Sensory mechanisms for animal orientation—can any new ones be discovered?. In *Animal migration, navigation and homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 25–34. Berlin: Springer-Verlag.
- Lohmann, K. J., Cain, D. C., Dodge, S. A. & Lohmann, C. M. F. 2001 Regional magnetic fields as navigational markers for sea turtles. *Science* **294**, 364–366.
- Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. & Swing, T. 2004 Geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909–910.
- Luschi, P., Del Seppia, C., Crosio, E. & Papi, F. 1996 Pigeon homing: evidence against reliance on magnetic information picked up en route to release sites. *Proc. R. Soc. B* **263**, 1219–1224.
- Martin, G. R. 1991 Ornithology—the question of polarization. *Nature* **350**, 194.
- Mouritsen, H. & Larsen, O. N. 2001 Migrating songbirds tested in computer-controlled Emlen funnels use stellar cues for a time-independent compass. *J. Exp. Biol.* **204**, 3855–3865.
- Mouritsen, H., Huyvaert, K. P., Frost, B. J. & Anderson, D. J. 2003 Waved albatrosses can navigate with strong magnets attached to their head. *J. Exp. Biol.* **206**, 4155–4166.

- Nevitt, G. A. 1999 Foraging by seabirds on an olfactory landscape. *Am. Sci.* **87**, 46–53.
- Nevitt, G. A. 2000 Olfactory foraging by Antarctic procellariiform seabirds: life at high Reynolds numbers. *Biol. Bull.* **198**, 245–253.
- Nevitt, G. A. & Bonadonna, F. In press. Seeing the world through the nose of a bird: new developments in the sensory ecology of procellariiform seabirds. *Mar. Ecol. Prog. Ser.*
- Nevitt, G. A., Veit, R. R. & Kareiva, P. 1995 Dimethyl sulphide as a foraging cue for Antarctic procellariiform seabirds. *Nature* **376**, 680–682.
- Papi, F., Luschi, P., Åkesson, S., Capogrossi, S. & Hays, G. C. 2000 Open-sea migration of magnetically disturbed sea turtles. *J. Exp. Biol.* **203**, 3435–3443.
- Phillips, J. B. & Waldvogel, J. A. 1988 Celestial polarized light patterns as a calibration reference for the sun compass of homing pigeons. *J. Theor. Biol.* **131**, 55–67.
- Ritz, T., Thalau, P., Phillips, J. B., Wiltschko, R. & Wiltschko, W. 2004 Resonance effects indicate a radical-pair mechanism for avian magnetic compass. *Nature* **429**, 177–180.
- Roberts, S., Guilford, T., Rezek, I. & Biro, D. 2004 Positional entropy during pigeon homing. I. Application of Bayesian latent state modelling. *J. Theor. Biol.* **227**, 39–50.
- Steiner, I., Bürgi, C., Werffeli, S., Dell’Omo, G., Valenti, P., Tröster, G., Wolfer, D. P. & Lipp, H. P. 2000 A GPS logger and software for analysis of homing in pigeons and small mammals. *Physiol. Behav.* **71**, 589–596.
- Walcott, C. 1996 Pigeon homing: observations, experiments and confusions. *J. Exp. Biol.* **199**, 21–27.
- Wallraff, H. G. 1999 The magnetic map of homing pigeons an evergreen phantom. *J. Theor. Biol.* **197**, 154–158.
- Wallraff, H. G. 2001 Navigation by homing pigeon: updated perspective. *Ethol. Ecol. Evol.* **13**, 1–48.
- Wallraff, H. G. 2004 Avian olfactory navigation: its empirical foundation and conceptual state. *Anim. Behav.* **67**, 189–204.
- Wallraff, H. G. & Andreae, M. O. 2000 Spatial gradients in ratios of atmospheric trace gases: a study stimulated by experiments on bird navigation. *Tellus B* **52**, 1138–1156.
- Warham, J. 1996 *The behaviour, population biology and physiology of the petrels*. London: Academic Press.
- Weimerskirch, H., Salamolard, M., Sarrazin, F. & Jouventin, P. 1993 Foraging strategy of wandering albatrosses through the breeding season: a study using satellite telemetry. *Auk* **110**, 325–342.
- Weimerskirch, H., Doncaster, C. P. & Cuenot-Chaillet, F. 1994 Pelagic seabirds and the marine environment: foraging patterns of wandering albatrosses in relation to prey availability and distribution. *Proc. R. Soc. B* **255**, 91–97.
- Weimerskirch, H., Mougey, T. & Hindermeier, X. 1997 Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behav. Ecol.* **8**, 635–643.
- Weimerskirch, H., Bonadonna, F., Bailleul, F., Mabile, G., Dell’Omo, G. & Lipp, H. P. 2002 GPS tracking of foraging albatrosses. *Science* **295**, 1259.
- Wiltschko, W. 1978 Further analysis of the magnetic compass of migratory birds. In *Animal migration, navigation and homing* (ed. K. Schmidt-Koenig & W. T. Keeton), pp. 302–310. Berlin: Springer Verlag.
- Wiltschko, W. & Wiltschko, R. 1972 Magnetic compass of European robins. *Science* **176**, 62–64.
- Wiltschko, W. & Wiltschko, R. 1996 Magnetic orientation in birds. *J. Exp. Biol.* **199**, 29–34.
- Wiltschko, R. & Wiltschko, W. 2003 Avian navigation: from historical to modern concepts. *Anim. Behav.* **65**, 257–272.
- Wiltschko, W., Traudt, J., Gunturkun, O., Prior, H. & Wiltschko, R. 2002 Lateralization of magnetic compass orientation in a migratory bird. *Nature* **419**, 467–470.
- Wiltschko, W., Munro, U., Ford, H. & Wiltschko, R. 2003 Lateralisation of magnetic compass orientation in silvereyes, *Zosterops lateralis*. *Aust. J. Zool.* **51**, 597–602.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.